Adaptive individual differences

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Chapter 2

The evolution of animal personalities

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ABSTRACT

In many animal species, individuals differ consistently in their behavioural tendencies, and the behaviour in one context is correlated with that in other contexts. From an adaptive perspective, the evolution of such personalities is still not well understood, because in many situations a more flexible structure of behaviour should provide a selective advantage. In this chapter we review several mechanisms that may contribute to an adaptive explanation of animal personalities. We focus on three basic questions. First, which factors favour the evolution of behavioural variation? Second, which factors favour the evolution of time-consistent behaviour? And third, which factors favour behavioural correlations across contexts?

Concerning the causes of variation we discuss the role of frequency-dependent selection and spatiotemporal variation in the environment. Variation can be the outcome of selection when each behavioural type has a fitness advantage when rare; when individuals facing an unpredictable environment play a bet-hedging strategy; or when different behavioural types complement each other in a synergistic way (e.g., division of labour).

Concerning the causes of correlations we address the role of architectural constraints, adaptation to the local habitat, and differences in state among individuals. We argue that behavioural correlations are unavoidable if individual behaviour is governed by a limited number of control variables (e.g., hormones) and then ask the question why the number of control variables is apparently quite small. Correlations are also to be expected when individuals differ in state and the optimal phenotype is state-dependent. Time-consistent behaviour will often result from positive feedbacks (e.g., due to learning) where state and behaviour reinforce each other.

INTRODUCTION

In many animal species, individuals of the same sex, age and size differ consistently in whole suites of correlated behavioural tendencies, comparable to human personalities (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*, 2004b). Examples abound. Birds often differ consistently in the way they explore their environment and these differences are associated with, for example, differences in boldness and aggressiveness (Groothuis & Carere, 2005). Rodents as mice and rats differ consistently in the way they deal with environmental challenges and such differences encompass, for example, differences in attack, avoidance and nest-building behaviour (Koolhaas *et al.*, 1999). Interestingly, personality differences are often associated with morphological (Ehlinger & Wilson, 1988), physiological (Korte *et al.*, 2005) and cognitive (Reddon & Hurd, 2009) differences among individuals. In this chapter we focus on the evolutionary causes of animal personalities (Wilson, 1998; Buss & Greiling, 1999; Dall *et al.*, 2004) What are the factors promoting the evolution of personalities? And how do these factors shape the structure (what type of traits are associated with each other?) and ontogenetic stability of personalities?

Understanding the evolution of animal personalities (henceforth personalities) requires a shift in our thinking about animal behaviour (Wilson, 1998). While behavioural ecologists have traditionally "atomized" the organism into single behavioural traits that are studied in isolation (Gould & Lewontin, 1979), the study of personalities requires a more holistic approach for at least two reasons. First, personalities refer to suites of correlated traits that are stable across (at least part of) the ontogeny of individuals (Sih *et al.*, 2004a; Sih *et al.*, 2004b). Consequently, interdependencies between multiple different traits (e.g., how does the boldness of an individual affect its aggressiveness and exploration behaviour) and the same trait expressed at different points during ontogeny (e.g., how does juvenile aggressiveness affect adult aggressiveness) have to be taken into account. Second, on a proximate level, trait correlations are often caused by genetic (Mackay, 2004), hormonal (Ketterson & Nolan, 1999) or cognitive mechanisms (Rolls, 2000) affecting multiple traits at the same time. In order to understand the evolution of such trait correlations we need an approach that integrates mechanisms and adaptation (Tinbergen, 1963; McNamara & Houston, in press).

What we need to understand: taking a closer look

Personalities refer to differences in suites of correlated behavioural traits that are stable across part of the ontogeny of individuals. In some cases, personality differences are associated with differences in the morphological (Ehlinger & Wilson,

1988), physiological (Koolhaas *et al.*, 1999), cognitive (Howard *et al.*, 1992) or environmental (Wilson, 1998) condition that individuals face, that is, with differences in state (McNamara & Houston, 1996). Some state differences are readily observable (e.g., differences in size, sex, position in dominance hierarchy), others are much less conspicuous (e.g., differences in nutrition, stress response system or level of experience with a particular behaviour).

The state of an individual affects the cost and benefits of its actions, and thus its optimal behaviour (McNamara & Houston, 1996; Houston & McNamara, 1999; Clark & Mangel, 2000). Consequently, individuals should adjust their behaviour to their current state, a phenomenon termed state-dependent behaviour (condition-dependent behaviour, phenotypic plasticity). Importantly for personalities, single states often affect the costs and benefits of multiple behavioural traits at the same time (McNamara & Houston, 1996). Differences in states thus provide a potentially powerful explanation for differences in suites of correlated behavioural traits.

Explaining personalities in terms of differences in state, however, requires us to provide answers to two basic questions. First, why do individuals differ in states in the first place? In many cases, the maintenance of such differences seems puzzling. Why, for example, should individuals differ in physiological characteristics as stress responsiveness (Aron & Aron, 1997; Koolhaas *et al.*, 1999) or basal metabolic rate (Careau *et al.*, 2008)? Second, why are such differences stable over time? Many states (e.g., energy reserves, experience with a particular behaviour, future fitness expectation) are affected by many different factors, including an individual's own behaviour. Such states are potentially highly variable over time. Why, then, should differences in states be stable over time and what are the mechanisms that give rise to such stability?

Differences in state thus provide a plausible explanation for personality differences (Dall *et al.*, 2004; Sih & Bell, 2008), but only a partial one. Personality differences can also be observed for individuals that do not seem to differ in state. In fact, many empirical studies that report personality differences aim to control for state differences among individuals.

The observation of personalities among individuals that do not differ in states is particularly puzzling. First, why should individuals differ in their response to the same decision problem (e.g., how to explore an environment) when facing identical costs and benefits associated with behavioural actions? Should we not rather expect that any given decision problem has a unique best behavioural solution which in turn outcompetes all others over evolutionary time? Second, why are the responses to different decision problems associated with each other in a correlative way (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*,

2004b)? Why should a bold individual, for example, be more aggressive than its shy conspecific and why should bold individuals tend to be bold throughout ontogeny? Such limited plasticity seems especially surprising since behaviour, in contrast to many morphological features, is often thought to be potentially highly plastic (but see DeWitt *et al.*, 1998). Shouldn't then a more flexible phenotype, that adjusts its behaviour to the current condition be advantageous (Wilson, 1998; Dall *et al.*, 2004)?

These are the type of questions we address in this chapter. To structure our thinking we will group our discussion under the two main themes of variation and correlation, reflecting two main aspects of personalities. We first focus on the causes of variation within populations. In particular, we discuss how random causes, frequency-dependent selection and spatiotemporal variation in the environment can give rise to variation in behaviour and states underlying behaviour. We then focus on the two types of behavioural correlations that are defining for personalities, correlations over time and across contexts. In particular, we will discuss the role of the architecture of behaviour, stable state differences and social conventions in causing stable behavioural correlations.

CAUSES OF VARIATION

Individuals can differ substantially in their behavioural response when confronted with the same decision problem (e.g., how to explore an environment, how to respond to a predator) and such behavioural variation is a key feature of personalities (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*, 2004b). Behavioural variation can take various forms. In some cases, variation is best depicted as a broad unimodal distribution (e.g., variation in many human personality traits, (Nettle, 2006)), in other situations, a small number of discrete variants coexist (e.g., variation in mating strategies, (Gross, 1996)). As discussed above, behavioural variation may or may not be associated with variation in states among individuals. Moreover, behavioural variation may or may not be associated with genetic variation (Wilson, 1994b; Bouchard & Loehlin, 2001).

In this section we focus on the on the ultimate causes of behavioural variation. As we have emphasized above, behavioural variation is often caused by variation in states and state-dependent behaviour and we briefly discuss the two main routes to state differences among individuals, evolved vs. random state differences. We then discuss two basic mechanisms that can give rise to adaptive variation in behaviour, frequency-dependent selection and spatiotemporal variation in the environment.

Differences in states

State differences among individuals are ubiquitous: pick any two individuals within a population and you typically find that these individuals differ in some aspects of their morphological, physiological, cognitive or environmental condition. Through their effect on the costs and benefits of behavioural actions such state differences are an important source of adaptive behavioural differences. In many situations aspects of the state of an individual are under the direct control of that individual. Individuals typically have, for example, the choice among different environmental conditions (e.g., habitats, social environments) or the choice how to fine-tune certain aspects of their physiological systems (e.g., stress responsive system, basal metabolic rate). Why should individuals that do initially not differ in states differ in such choices? At first sight, one would perhaps expect that there is one best choice for any choice among different states.

In what follows, we discuss two main routes that give rise to adaptive variation in states, frequency-dependent selection and spatiotemporal variation. State differences among individuals, however, need not always reflect adaptive evolution. In many situations, aspects of the state of an individual are affected by factors that are not under the control of the individual. Differences in states arise whenever these factors differ between individuals. One individual, for example, grows up in a rich environment while another grows up in a poor environment. One individual finds a high-quality food source and thus increases its nutritional condition while another one does not find such a food source. One individual gets infected by a parasite while another one does not. Examples of state differences caused by such random factors abound.

Frequency-dependent selection

In groups of foraging animals, individuals typically have the choice between two different behavioural roles (Giraldeau & Beauchamp, 1999), an individual can either search for food sources on its own ("producer") or exploit food sources discovered by others ("scrounger"). Producer-scrounger situations (Barnard & Sibly, 1981) are a prototype example in which the benefits associated with a phenotype depend negatively on the frequency of that phenotype in the population: the higher the frequency of scroungers in a group, the less beneficial this role becomes, since more scroungers compete for fewer resources. Such situations give rise to so-called negative frequency-dependent selection (Maynard Smith, 1982), a form of selection that is known to be an important source of variation within populations (Heino *et al.*, 1998; Dugatkin & Reeve, 2000; Sinervo & Calsbeek, 2006).

In situations with negative frequency-dependence selection, selection acts to increase the frequency of rare phenotypes within populations. In its simplest form,

as in the producer-scrounger example above (Barnard & Sibly, 1981), this rareness advantage gives rise to two phenotypes that coexist in stable frequencies within a population. Moreover, whenever individuals have the choice between more than two phenotypes, negative frequency dependence can give rise to situations in which any number of phenotypes can coexist in stable frequencies. When negative frequency dependence interacts with positive frequency dependence, as for example in the so-called rock-scissor-paper games (Maynard Smith, 1982), selection can give rise to a dynamic equilibrium in which multiple phenotypes coexist at continuously changing frequencies (Sinervo & Lively, 1996; Sinervo & Calsbeek, 2006).

Negative frequency-dependent selection can, as in the producer-scrounger game above, give rise to adaptive behavioural variation among individuals that do initially not differ in states. The same process can also give rise to adaptive state differences among individuals. The benefits to, for example, a particular physiological or cognitive architecture (e.g., particular level of stress responsiveness, particular learning rule) might depend on how common this architecture is in the population, thus promoting the coexistence of different architectures (Wolf *et al.*, 2008b). Similarly, the benefits of being in a particular environment (e.g., territory, habitat or social position) might depend on the frequency with which other individuals choose this environment, thus promoting the coexistence of individuals in different environmental states (Ens *et al.*, 1995; Wilson, 1998).

Negative frequency-dependent selection is a common phenomenon in social interactions (Maynard Smith, 1982; Svensson & Sheldon, 1998; Dugatkin & Reeve, 2000). It occurs, for example, in direct interactions among individuals if there is an inherent benefit to adopt a different phenotype to that of the interacting partners. Such situations occur in agonistic interactions, as for example hawk-dove like encounters (Maynard Smith, 1982), in which the aggressive hawk strategy is beneficial whenever the opponent plays dove, whereas the non-aggressive dove strategy is beneficial whenever the opponent plays hawk. They also occur in more cooperative interactions, when social partners benefit from diversifying into different behavioural roles that complement each other (Clark & Ehlinger, 1987). The benefits of such behavioural complementation can be caused by various mechanisms. Choosing different behavioural roles may help, for example, to avoid competition among partners, to reap the benefits of behavioural specialization or to reduce the risk associated with a certain strategy.

Negative frequency dependence can also be caused more indirectly (Kokko & Lopez-Sepulcre, 2007) via competition for different types of resources that have density dependent benefits (i.e., the benefits of a resource decrease with the number of individuals that compete for that type of resource). Such density dependence gives rise to negative frequency dependence: the more individuals that compete for

a particular type of resource (e.g., territory, habitat, mate) the less beneficial it becomes. Density-dependent resource competition can thus promote the coexistence of individuals that choose for different resources (Wilson, 1998), which in turn gives rise to adaptive differences in states and behaviour among individuals.

Negatively frequency-dependent selection can thus give rise to adaptive variation in states and/or behaviour among individuals. In principle, this variation might or might not be associated with genetic variation (Maynard Smith, 1982; Wilson, 1994b). Consider, for example, a situation in which two phenotypes coexist with frequencies of 30% and 70% (e.g., producer and scroungers, individuals with a low and a high basal metabolic rate or slow and fast learners). This phenotypic variation can arise both in a population of genetically identical individuals that adopt each of the phenotypes randomly but with the same probability (choose one phenotype in 30%, the other in 70% of the cases) or in a genetically polymorphic population in which a fixed proportion of individuals adopts each of the phenotypes (30% of the individuals choose one phenotype, 70% the other).

Individual differences in foraging behaviour in the larval fruitfly (*Drosophila melanogaster*) provide a good example of the latter situation (Fitzpatrick *et al.*, 2007). In natural population, a dimorphism in foraging strategies can be observed ("rover" vs. "sitter" individuals). This dimorphism is based on a single major gene polymorphism that is maintained by negative frequency-dependent selection, both the rover and the sitter allele attain their highest relative fitness when rare in the population.

Spatiotemporal variation in the environment

Evolution shapes the phenotype of individuals to match their environment, and in many natural situations, the environment and, thus, the optimal phenotype, varies in space or in time. What is the expected evolutionary outcome in such a situation? In particular, should we expect that, as it is often thought to be the case (Nettle, 2006; Koolhaas *et al.*, 2007; Penke *et al.*, 2007), environmental variation promotes phenotypic variation within populations? And if so, should we expect that such phenotypic variation is associated with genetic variation?

It turns out that the answers to these questions depend on the details of the situation (Hedrick *et al.*, 1976; Hedrick, 1986; Seger & Brockmann, 1987; Moran, 1992; Leimar, 2005), in particular, on whether the population faces spatial or temporal variation in the environment (for an alternative classification see Frank & Slatkin, 1990; Donaldson-Matasci *et al.*, 2008) and on how well individuals can match their phenotype to their environment.

To see the importance of phenotype-environment matching consider first a situation in which individuals can match their phenotype to their environment in

an error and cost-free manner, be it via habitat choice (i.e., the environment is chosen to match the phenotype), phenotypic plasticity (i.e., the phenotype is chosen to match the environment) or a combination of both. In such a situation evolution is expected to result in perfect phenotype-environment matching. No variation is maintained within each environment. This example is certainly extreme and unrealistic (DeWitt *et al.*, 1998), it illustrates, however, that environmental variation can only give rise to phenotypic variation within environments in situations with limited phenotype-environment matching.

Consider now the most basic scenario of spatial variation. A population inhabits an environment with two types of habitats, different phenotypes are favoured within each habitat. As we have just seen, if perfect phenotype-environment matching is possible, no variation within environments can be maintained. This is different in situations with an intermediated degree of phenotype-environment matching, that is in situations where habitat choice or phenotypic plasticity is possible but not perfect. Individuals might, for example, make errors when choosing habitats. In such situations phenotypic variation can be maintained both at a population level and within each habitat (Seger & Brockmann, 1987). The reason for this is as follows. Since some degree of phenotype-environment matching is possible, coexisting genotypes (or phenotypes of a plastic genotype) experience different environments, each genotype will, on average, experience more often that environment in which it is favoured. Variation within environments arises since phenotype-environment matching is not perfect. The resulting phenotypic variation can in principle be due to plasticity, a genetic polymorphism or a combination of both factors.

A good example for adaptive variation caused by spatial variation in the environment is provided by the bluegill sunfish (*Lepomis macrochirus*) that inhabits North American freshwater lakes (Ehlinger & Wilson, 1988). In these populations, consistent individual differences in foraging tactics (e.g., hover duration, pattern of movement) have been described. It turns out that these differences can be associated with differences in habitat use: the most efficient foraging tactic depends on whether an individual is in littoral or open water zones and individuals that employ different tactics are preferentially (but not exclusively, thus phenotype-environment matching is not perfect) found in that habitat that fits their foraging tactic best. Interestingly, differences in foraging tactics are associated with rather subtle morphological differences (e.g., fin size, fin placement) between individuals, which again tend to favour one habitat over the other. We will return to this point below when discussing the causes of consistency.

Spatial variation need not correspond to differences in the abiotic environment, as above, but can also be induced by variation in the biotic environment of indi-

viduals. It has been suggested, for example, that variation in neuroticism in humans is maintained by the fact that high levels of neuroticism are beneficial in predatory environments, whereas low levels of neuroticism are favoured in predator-free environments (Nettle, 2006).

In addition to spatial variation, also temporal variation in environmental conditions has often been suggested to contribute to the maintenance of personality differences. However, exactly as for spatial variation, the evolutionary effects of temporal fluctuations depend on population regulation, the scope for phenotype-environment matching, the costs of plasticity, and many other details of the biological system under consideration. To see this, consider a simple scenario of temporal fluctuations. Each generation all individuals within a population face the same environment , but the environment varies across generations, and different environments favour different phenotypes. As we have seen above, whenever individuals can adjust their phenotype to their current environment in an error and cost-free manner, no variation is maintained within environments. However, unlike for spatial variation, genetic variation cannot be maintained in situations with limited phenotype-environment matching, at least as long as generations are non-overlapping (see the discussion of bet-hedging below for how purely phenotypic variation can be maintained in such a scenario). The reason is as follows. All genotypes face exactly the same environment, there is no frequency dependence and among any number of potential genotypes there will typically be exactly one that achieves the highest (geometric mean) fitness (Seger & Brockmann, 1987).

Many animal species, however, are iteroparous and have overlapping generations and if we allow for this, also temporal fluctuations can maintain genetic polymorphisms (Ellner & Hairston, 1994). The intuition is as follows. As the lifetime of individuals increases (and thus the generation overlap), temporal fluctuations tend to average out within the lifetime of a single individual and the model comes closer and closer to a temporal analogue of a spatial model without habitat choice which can maintain genetic polymorphisms in the case of local density dependence (Levene, 1953).

A well-known feature of temporally fluctuating environments, be it with or without overlapping generations, is that so called bet-hedging genotypes are selectively favoured (Seger & Brockmann, 1987), that is genotypes that switch during development stochastically between two or more phenotypes. A bet-hedging genotype thus gives rise to a mixture of phenotypes (e.g., aggressive and non-aggressive individuals, individuals with a low and a high stress responsiveness). This can be seen as a risk-spreading strategy, since no matter how the environment turns out, some of the bet-hedging phenotypes are well adapted. More tech-

nically, a diversifying bet-hedger can reduce its variance in fitness in an optimal way and thereby increase its geometric mean fitness.

In summary, in species with non-overlapping generations, temporal fluctuations can only maintain phenotypic variation. In species with overlapping generations, also genetic variation can be maintained, but again, bet-hedging strategies are selectively favoured (Leimar, 2005).

Temporal fluctuations need not be restricted to the abiotic environment of individuals. Dingemanse and colleagues, for example, studied a population of great tits (*Parus major*) for which environmental conditions (masting of beeches) varied across years (Dingemanse *et al.*, 2004). They found that different behavioural types were favoured dependent on the environmental condition (in terms of adult survival and number of offspring surviving to breeding), which in turn might explain the maintenance of variation in this populations.

Temporal fluctuations can also arise through the social environment of individuals. Mouse populations, for example, are known to go through phases of growth and decline. It has been hypothesized that these fluctuations can explain the maintenance of genetic variation in aggressiveness in such populations since the extreme phenotypes have differential fitness at different population densities (Chitty, 1967; Van Oortmerssen & Busser, 1989). Recent research on populations of western bluebirds (*Sialia mexicana*) points in a similar direction (Duckworth & Badyaev, 2007). During range expansions across the north-western United States highly aggressive individuals were selectively favoured when colonizing new populations since those individuals could more easily displace less aggressive mountain bluebirds. Once mountain bluebirds were displaced, however, high levels of aggression were selectively disfavoured, presumably because aggressive individuals provide almost no parental care. Such temporal variation in selection pressures might thus explain the maintenance of variation in aggressiveness within these populations.

CAUSES OF CORRELATIONS

Up to now we focussed on the causes of behavioural differences for particular decision problems (e.g., how to explore an environment, how to respond to a predator). Personalities, however, refer to much more than such behavioural differences (Clark & Ehlinger, 1987; Digman, 1990; Gosling, 2001; Sih *et al.*, 2004b). First, personalities refer to behavioural differences that are stable through part of the ontogeny of individuals (time-consistency of behaviour), that is, individuals that score relatively high (low) in a given behavioural situation often tend to score

relatively high (low) in the same situation at later points in time. Second, personalities refer to behavioural differences that extend to whole suites of correlated behaviours, that is, correlated variation in functionally different contexts (e.g., antipredator behaviour is correlated with contest behaviour).

Both types of correlations indicate behavioural inflexibilities (Wilson, 1998; Dall *et al.*, 2004) in the sense that the behaviour that an individual exhibits at one point in time and in one particular context is predictive for the same individual's behaviour at later points in time and in different contexts. Why did evolution give rise to such behavioural inflexibilities? Why should an individual stickleback that is, for example, relatively aggressive at one point in time also be relatively aggressive at later points in time (Bakker, 1986)? And why should aggressive individuals also be bolder than their non-aggressive conspecific (Huntingford, 1976)? It would seem that a flexible structure of behaviour is more advantageous.

To answer these questions, we first explore why, in some cases, evolution gives rise to architectures of behaviour that result in apparently maladaptive behavioural correlations. We then focus on state variables as a cause of behavioural correlations in general and discuss two main sources for the stability of state differences over time, inherently stable state differences and positive feedback mechanisms. Behavioural correlations need not reflect underlying state variables and we conclude this section by discussing how social conventions can give rise to adaptive behavioural correlations.

Architectur of behaviour

On a proximate level, the behavioural phenotype of an individual is affected by its architecture of behaviour, that is, the genetic, physiological, neurobiological and cognitive systems underlying its behaviour. This architecture, in turn, gives rise to behavioural correlations whenever multiple traits are affected by a common underlying mechanism within this architecture. Such common mechanisms are ubiquitous, examples include pleiotropic genes (Mackay, 2004), hormones (Ketterson & Nolan, 1999), neurotransmitters (Bond, 2001), behavioural rules (Todd & Gigerenzer, 2000) and emotions (Rolls, 2000) that affect multiple traits at the same time.

It has been shown, for example, that the positive correlation of aggressiveness through ontogeny in the three-spined stickleback (*Gasterosteus aculeatus*) is caused by pleiotropic genes (Bakker, 1986). Pleiotropic genes are also thought to be responsible (Riechert & Hedrick, 1993; Maupin & Riechert, 2001) for the positive correlation between agonistic behaviour, antipredator behaviour and superfluous killing in the American desert spider (*Agelenopsis aperta*). The negative correlation between mating effort and parental effort in several bird species is caused by the

hormone testosterone (McGlothlin *et al.*, 2007). And finally, the fearfulness of an individual affects its reaction to a multitude of potentially threatening situations, including persistent dangers in its ecology, novelty and interactions with conspecifics (Boissy, 1995).

Behavioural correlations can thus be the result of a relatively rigid architecture of behaviour. The resulting behavioural associations appear adaptive in some cases (see below), in others, however, they give rise to apparently maladaptive behaviours (Sih *et al.*, 2004a). It might, for example, be advantageous for a female spider to show high levels of aggression towards territorial intruders, but why should such individuals also kill and consume all potential mates during courtship and as a consequence be left unmated at the time of egg laying (Arnqvist & Henriksson, 1997)? Similarly, it might be advantageous for a salamander larvae to be relatively active in the absence of predatory cues but why should such individuals also be relatively active in the presence of such cues (Sih *et al.*, 2003)? In other words, rigid behavioural architectures can explain behavioural correlations at the proximate level, but from an ultimate perspective, one is tempted to ask why such rigid behavioural architectures persist over evolutionary time. Especially in cases where a rigid architecture gives rise to apparently maladaptive behaviour, one would expect evolution to uncouple unfavourable behavioural associations.

The evolution of a more flexible behavioural architecture might in principle be prevented for two types of reasons. First, a more flexible architecture might be advantageous (i.e., an individual with such an architecture would achieve a higher fitness than an individual with a more rigid architecture) but not attainable by evolution. Such a situation can occur because the evolutionary transition from one complex phenotype (here: rigid architecture) to another complex phenotype (more flexible architecture) is typically not possible in one step but requires many intermediate steps. The architectures associated with these intermediate steps, however, might be disadvantageous to the individual. In other words, the evolution of a more flexible behavioural architecture might be associated with crossing an adaptive valley of the fitness landscape which in turn prevents the evolution of a more flexible behavioural architecture. Such a situation occurs if the current behavioural correlations correspond to a local peak in the fitness landscape, reflecting the fact that the involved traits are to some extent well adapted to each other. Second, a more flexible behavioural architecture might not be advantageous, that is an individual with such an architecture would achieve a lower fitness than an individual with a more rigid architecture. Such a situation can occur if a more flexible architecture is associated with costs (e.g. costs of plasticity, DeWitt *et al.*, 1998) that are not outweighed by the corresponding benefits. In both

cases, trait correlations can persist even though they give rise to behavioural traits that, when viewed in isolation from their architectural basis, might appear maladaptive.

Stable state variables

Many aspects of the state of an individual affect the cost and benefits of multiple behavioural traits at the same time (McNamara & Houston, 1996). Consequently, individuals should make these behaviours dependent on their current state. State differences in combination with state-dependent behaviour (condition-dependent behaviour, phenotypic plasticity) thus provide a natural explanations for adaptive behavioural correlations of apparently unrelated behavioural traits. However, state differences do not immediately explain why individuals should be consistent over time. Put differently, why should initial state differences among individuals be relatively stable over time? In this section we discuss two main roads to consistency of states, inherently stable state variables and positive feedback mechanisms between state and behaviour.

INHERENTLY STABLE STATE VARIABLES

As we have discussed above, random causes, frequency-dependent selection and spatiotemporal variation can give rise to populations with variation in states among individuals. Whenever a change of state among these variants is associated with substantial costs, such situations can result in consistent differences in state and, consequently, consistent differences in whole suites of (state-dependent) traits that are affected by this state.

In some situations, differences in states are associated with differences in morphological and physiological characteristics that are costly to change. Consider, for example, sex differences. In many animal species, frequency-dependent selection maintains two sexes at constant proportions within populations. These equilibrium proportions can in principle be maintained in populations in which individuals change their sex over time. Such a sex change, however, is often associated with substantial costs to the individual (caused by the necessary morphological and physiological changes). We thus typically observe stable (life long) sex differences among individuals which are, in turn, associated with whole suites of correlated behavioural traits. In humans (Costa *et al.*, 2001), for example, women typically score higher than males on traits related to the agreeableness axis (e.g., cooperativeness, empathy, trust), in many other animal species, sex differences exist for example in parental care and courtship behaviour (Kelley, 1988).

In some situations, evolution gives rise to populations in which individuals are distributed among a small number of discrete size classes (Brockmann, 2001). A

change among these variants is typically associated with substantial costs, which in turn favours consistency in size and thus consistency in behavioural traits that are affected by body size. A common phenomenon, for example, is the use of fighting or sneaking as an alternative mating tactic depending on body size, as observed in dung beetles, bees, and many other species (Gross, 1996).

Morphological and physiological differences, which can only be changed under substantial costs, need not be as conspicuous as in the case of sex or size differences. As discussed above (Ehlinger & Wilson, 1988), within populations of bluegill sunfish (*Lepomis Macrochirus*) individuals differ in morphological characteristics that are functional either in the littoral or open water zone (e.g., fin size, fin placement). Such (stable) differences are associated with consistent differences behavioural traits, as for example foraging tactics. Interestingly, the underlying morphological differences are not obvious to an observer, in fact, sunfish have been studied for many years without recognizing the adaptive nature of these differences (Wilson, 1998).

Inherently stable state differences need not be associated with morphological and physiological characteristics that are costly to change. In some cases stability is caused (in part) by factors external to the individual. Human societies, for example, encompass a large diversity of social positions (e.g., teachers, managers, bureaucrats). While it is in principle possible for an individual to change its position, such changes are typically very costly to the individual (e.g., in terms of required training or education). As a result, individuals typically stick to their position once chosen. Consistent differences in such positions, in turn, are often associated with consistent differences in suites of correlated behavioural traits. Human leaders, for example, are more extrovert and more conscientious than non-leaders (Judge *et al.*, 2002); entrepreneurs are more conscientious and open, but less neurotic and agreeable than managers (Zhao & Seibert, 2006).

SELF-REINFORCING FEEDBACK LOOPS

Many aspects of the state of an individual are much more labile than the ones discussed above. Consider, for example, the energy reserves of an individual, the experience that an individual has with a certain behaviour or the future fitness expectations of an individual. These states are, like many others, labile since they can easily be changed by many different factors, including the individual's own behaviour.

Labile states can, as inherently stable states, affect multiple behavioural traits at the same time thus explaining suites of correlated behavioural traits. But why should labile states be stable over time? Differently asked, why should initial differences in such states among individuals be stable over time?

In some situations the state and behaviour of individuals are coupled by a positive feedback (Sih *et al.*, 2004b; Sih & Bell, 2008): initial state differences give rise to differences in behaviour which act to stabilize or even increase the initial state differences. Such positive feedback mechanism, in turn, can give rise to consistent individual differences in labile states and behavioural traits that are associated with these states.

An important positive feedback is the feedback between behaviour and the experience an individual has with this behaviour. Individuals often get better with increased experience (Rosenzweig & Bennett, 1996), that is, processes like learning, training and skill formation give rise to lower costs or higher benefits for the same action when repeated, which in turn favours consistency in this behaviour (Wolf *et al.*, 2008b).

Positive feedbacks via experience can give rise to consistent individual differences in single behavioural traits. Animals often learn how to recognize predators (Griffin, 2004), for example, which in turn makes it less costly to explore and forage a risky habitat for individuals that did this before. Under such conditions, whenever variation in risk-taking behaviour is maintained within populations (Wilson, 1998; Wolf *et al.*, 2007a), positive feedbacks acts to promote consistent individual differences in risk-taking behaviour.

Positive feedbacks can also give rise to consistent differences in suites of correlated behavioural traits. Experience gained in one context, for example, can affect the cost and benefits of behavioural actions in another context and thus give rise to a cross context association of behavioural traits. Individuals that learn to assess the strength of conspecific competitors might, for example, at the same time get better at assessing the risk associated with predators.

Positive feedback need not act via behaviour directly. The cost and benefits of behavioural traits that are related to resource acquisition (e.g., aggression, boldness), for example, often depend on characteristics of the individual that are affected by the resources available to an individual (e.g., size, strength, resource holding potential) and this interaction can give rise to a positive feedback loop (Sih & Bell, 2008). The strength of individuals positively affects its fighting ability, for example, which in turn gives rise to more resources that positively affect its strength. This feedback favours consistency in all kinds of traits related to the characteristic.

Positive feedbacks can also act via physiological characteristics of the individual. It has been suggested, for example, that in many animal species, deviations from a once chosen growth rate are costly to the individual (Stamps, 2007; Biro & Stamps, 2008). Compensatory growth, for example, often comes at the cost of increased risk of disease, higher mortality rates, or decreased physiological capac-

ity later in life (Mangel & Munch, 2005). Similarly, deviations from a once chosen basic metabolic rate or stress responsiveness might be costly to the individual. In such situations, consistency in such physiological characteristics (growth rate, basic metabolic rate, stress responsiveness) is favoured and thus consistency in suites of traits that are associated with these characteristics. Differences in growth rates, for example, affect the cost and benefits of all kinds of traits that are related to food intake as aggression and boldness (Stamps, 2007).

SOCIAL CONVENTIONS

An adaptive association of different behaviours need not reflect an underlying state variable that affects the costs and benefits of these behaviours, as in the situations discussed above. Rather, behavioural traits (be it the same trait expressed at different points during ontogeny or different traits) can get associated with each other because individuals in a population follow an adaptive behavioural rule (or convention) that favours the association of these traits.

When an individual is confronted with another individual in a social interaction, for example, it might make its behaviour dependent on the behavioural history of the other individual. To be concrete, when A and B interact in a hawk-dove like encounter (Maynard Smith, 1982), individuals might follow the rule "if the opponent played hawk before, choose dove, otherwise choose hawk". Such an eavesdropping strategy (Johnstone, 2001) makes sense whenever there is some consistency in the behaviour of individuals. Consistency thus favours eavesdropping since it allows the eavesdropper to choose the best response to the behaviour of its partner (e.g., choose hawk when confronted with a dove, otherwise choose dove). Conversely, eavesdropping favours consistency whenever it is beneficial for individuals to be predictable. This interaction between consistency and eavesdropping can thus give rise to populations in which individuals follow a behavioural rule that favours consistency and, as a result, individuals show consistent behaviour.

Do such conventions arise in natural situations? The so called winner-loser effect (Chase *et al.*, 1994) might be a good example. It is a well known phenomenon that winners of previous contests are more likely to win again (and losers are more likely to lose again), even against different opponents and in situations in which there are no asymmetries between the opponents. According to a survey across several taxa (Rutte *et al.*, 2006), when there are no other asymmetries between opponents, the probability of winning a subsequent contest is almost doubled for previous winners, but is reduced more than five times for previous losers even against different opponent. Winner-loser effects are currently not well understood but one explanation that is given by several authors is based on the

arguments above: the prior success of the opponent might act as a 'random historical asymmetry' that is used to settle the conflict (Parker, 1974; Maynard Smith & Parker, 1976; Hammerstein, 1981; Van Doorn *et al.*, 2003a; Van Doorn *et al.*, 2003b) Social conventions that favour consistency are not limited to aggressive interactions. An influential idea in explaining cooperation is that individuals should make their behaviour dependent on an image score of the other individual (Nowak & Sigmund, 1998; Leimar & Hammerstein, 2001), a measure of how cooperative the other individuals has been in the past. Such image scoring can, in turn, favour consistency in cooperative behaviour.

DISCUSSION

In this chapter, we have focussed on the evolutionary causes of personalities. The existence of personalities, however, should be expected to have consequences for evolutionary process (Wilson, 1998; Dall *et al.*, 2004). In social contexts, for example, the existence of variation in one trait often selects for variation in another trait. Variation in cooperativeness, for example, can select for variation in choosiness which in turn selects for cooperativeness (McNamara *et al.*, 2008). Importantly, variation in cooperativeness can thus trigger a coevolutionary process of cooperativeness and choosiness that give rise to very different evolutionary outcomes (here: high levels of cooperation) when compared to situations without such initial variation.

We aimed to provide on overview about the basic factors and mechanisms that promote the evolution of personalities. We focussed on two basic questions: which factors promote adaptive behavioural variation within populations and which factors promote adaptive correlations among behavioural traits, be it across contexts or over time?

Factors promoting variation and correlations can interact in various ways. Random causes, frequency-dependent selection and spatiotemporal variation can give rise to variation in states among individuals. Whenever such states affect the cost and benefits of behavioural traits, state differences promote state-dependent behaviour and thus adaptive behavioural variation or, whenever the costs and benefits of multiple behavioural traits are affected at the same time, adaptive behavioural variation that is correlated across contexts. In principle, behavioural variation should be expected to be stable as long as the underlying variation in states is stable. Whenever states are very costly to change and thus inherently stable (e.g., sex and size differences) variation is expected to be stable. In the case of labile states (e.g., energetic state, experience with a certain behaviour), variation

can be stabilized via positive feedback mechanisms between behaviour and states: variation in states gives rise to variation in behaviour that acts to stabilize or increase initial state differences.

Spatiotemporal variation and frequency-dependent selection can give rise to behavioural variation that is not associated with underlying state differences and state-dependent behaviour (e.g. producers and scroungers, hawks and doves). Such variation can be stabilized over time via positive feedback mechanisms: the initial variation in behaviour gives rise to differences in states that act to stabilize the behavioural differences (e.g., producers gain experience that makes producing more beneficial). Such feedbacks can also extend to multiple behavioural traits, thus giving rise to adaptive behavioural correlations (e.g. experience gained in producer-scrounger context can affect the cost and benefits of behaviour in different contexts). Alternatively, behavioural variation in single or multiple behavioural traits can be stabilized via social conventions which favour consistency in behaviour.

The above summary emphasizes that personalities ask for a holistic approach to behaviour. Rather than "atomizing the organism" (Gould & Lewontin, 1979) into single behavioural traits that are studied in isolation, multiple different traits have to be studied in concert: behaviour in one context (e.g., antipredator, mating, fighting, parental care) can often only be understood when taking the interdependencies with past and future behaviour in the same and other contexts into account. Personalities ask for an integration of mechanism and adaptation (Tinbergen, 1963; McNamara & Houston, in press). As we have emphasized above, behavioural correlations are often caused by the architecture of behaviour, that is by the genetic, physiological, neurobiological and cognitive systems underlying behaviour. In order to understand such correlations we thus have to understand the coevolution behaviour and mechanisms causing behaviour.